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Food and habitat specialization in coexisting springtails (Collembola, Entomobryidae)[1])

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With 5 figures

1. Introduction

Closely related species living in the same area tend to utilize different resources. Numerous examples of resource partitioning can be found in the literature (see review of Schoener 1974 and Pianka 1976) and can be classified under three general headings: food type, habitat and time. However, comparatively little is known about resource partitioning in soil arthropods. Usually a very low degree of food specialization is observed (Wallwork 1970, Luxton 1972, Anderson & Healey 1972, Anderson 1975) but as stated by Anderson (1978), the "dynamic mosaic" nature of soil and litter microhabitats might provide ample opportunities for resource partitioning and specialization in space and time.

In springtails, an important component in the litter fauna, large differences in transpiration rate (Verhoef & Witteveen 1980, Vegter & Huyer-Brugman 1983), related to physiological and behavioural adaptations to drought (Verhoef & Nagelkerke 1977, Joosse 1981, Verhoef & Li 1983) do often lead to differences in spatial distribution (Joosse 1970, Kaczmarek 1975, Verhoef & van Selm 1982). Moreover, specific differences in gut content are generally interpreted as microhabitat differences (Knight & Angel 1967, Gilmore & Raffensperger 1970, Petersen 1971, Anderson & Healey 1972). Temporal resource partitioning might also be possible in springtails. Clear differences in seasonal dynamics have been observed by Joosse (1969), Petersen (1980), Verhoef & van Selm (1982) and Vegter (in prep.).

Differences in resource utilization are often attributed to competitive pressures. However, the validity of a resource partitioning study does not depend on the demonstration of interspecific competition for limiting resources (Thomson 1978). Recently, the importance of interspecific competition in animal communities has even been questioned (Connel 1975, Wiens 1977, Birch 1979, Taylor 1980). Lawton & Strong (1981) stressed the importance of physiological limitations and natural enemies in the formation of community patterns, in folivorous insects. However, any statement about the importance of processes underlying community patterns can only be made after detailed investigations of differences in resource use in coexisting species.

The object of the study reported in this paper is to find differences in resource use between coexisting surface dwelling springtails (Entomobryidae). The major part of the paper will deal with food and spatial distribution of *Orchesella cincta* (Linné) and *Tomocerus minor* (Lubbock). The physiological ecology of these species has been studied extensively (see Joosse 1981, for a review), and much is known about their seasonal dynamics (van Straalen 1983) in a woodland area adjacent to the one studied in this paper.

[1]) Contribution to the Vth International Colloquium on Apterygota, Louvain-La-Neuve (23—26 August, 1982) organized by C. Grégoire-Wibo and Ph. Lebrun.

2. Materials and methods

2.1. General note

The woodland area studied is a moist pine plantation in the Flevopolders, the Netherlands. The plantation is dominated by *Pinus nigra* (ARN.) (var. *austriaca* A. et G.). There is no undergrowth, and trees are evenaged and equidistant. Five species of surface dwelling springtails (Entomobryidae) are found in this area: *Tomocerus minor* (LUBBOCK), *Orchesella cincta* (LINNÉ), *Orchesella villosa* (GEOFFROY), *Entomobrya nivalis* (LINNÉ) and *Lepidocyrtus violaceus* (LUBBOCK).

2.1. Gut content analysis

Springtails were sieved out of the litter layer present in a 30 cm ⌀ core sampler, and stored in GISIN's preservative fluid (GISIN 1960). On three occasions (May 14, May 28 and June 12, 1980) four samples were taken. The gut content of ten individuals per species from each sample were dissected and suspended individually in a small drop of water. Individuals with half-filled gut were discarded. The suspensions were examined under a microscope (magnification: 400×). Food items were scored when they crossed the middle of the micrometer fitted in the eyepiece, during a scan along a random chosen line. At least fifty items per gut were scored. The same procedure was applied to the guts of individuals of *T. minor* and *O. cincta* held in laboratory cultures. These animals were fed with small twigs overgrown with a mixture of fungi and green algae (*Pleurococcus* spec.). Since microhabitat segregation is ruled out, comparisons between gut contents in the lab might provide some insight in food preferences.

2.2. Spatial distribution

The woodland area studied was bordered by open field at the north and west side (Fig. 1). From these exposed edges towards the centre of the woodland light intensity and wind speed decrease gradually. This will in turn influence other environmental factors, like temperature and in particular the gradient in vapor pressure present in the litter layer. This gradual change from edge to central area is punctuated by influences of the tree trunks. The microclimate in the litter layer near a tree trunk might be very different. This pattern in the abiotic environment gave rise to two sampling schemes. First the effect of the edge vs. the central part of the area, and the effect of trees on abundance of the dominant species, *O. cincta* and *T. minor* was investigated by random sampling with a 10 cm ⌀ diameter core sampler (internal surface 72.4 cm²). 18 samples were taken at the tree base (5—15 cm from the trunk) and 18 samples between trees. In total 22 samples were taken from the area labeled "edge" (Fig. 1) and 14 from the "centre" part.

To study the effect of the gradual transition from edge to centre of the plot in more detail, 3 parallel rows of 8 equidistant samples were taken, as indicated in Fig. 1 by "transects". As springtail abundance appeared to be higher near trees (see results) samples were taken at the tree base. This sampling scheme was performed twice. In summer a 10 cm core sampler was used, in winter a 25×25 cm sampler, in view of the lower abundance of springtails in this season. To equalize the sample surfaces of winter and summer, the results of the winter sampling will be multiplied by

$$\frac{72.4}{625}$$

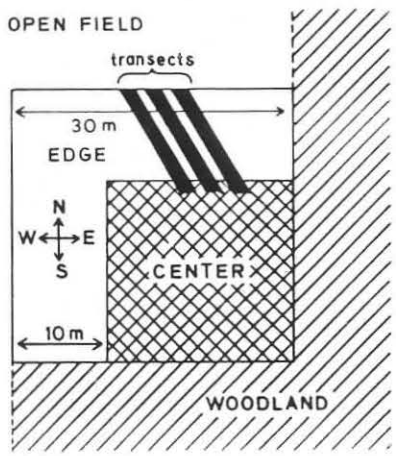

Fig. 1. Plan of the woodland area and lay-out of the sampling schemes.

The soil fauna was extracted by a modified TULLGREN-funnel (VAN STRAALEN & RIJNINKS 1982). Since differences in spatial distribution might be related to differences in drought-tolerance between species, measurements of transpiration rates were performed using procedures outlined by VEGTER & HUYER-BRUGMAN (1983).

2.3. Statistical methods

The effects of trees and edge vs. central area on abundance of *Tomocerus minor* and *Orchesella cincta* are evaluated by a threeway ANOVA with repeated measured on the factor "species". Since abundance estimates for both species are based on the same samples, they will not be independent, and can be seen as repeated measures of springtail abundance. Computational procedures for this design can be found in WINER (1971). A $\ln(N + 1)$ transformation (N = sample count) was applied to the sample counts before analysis, in order to fulfil the assumptions for the ANOVA: normality and homogeneity of variances. The use of repeated measurement designs involves two other assumptions about the structure of the variance-covariance matrices of the repeated measures for each factor combination (WINER 1971). These criteria were met since the factor species is repeated only once and the correlation coefficients between the two species were not inhomogeneous.

Other statistical procedures used in this paper are of exploratory nature. They will be useful to bring out the pattern present in the data. Significance testing will be omitted in these cases.

3. Results

3.1. Gut contents of *O. cincta* and *T. minor*

Quite a large number of individuals of both species had empty guts. Only 39% of *O. cincta* and 58% of *T. minor* had totally filled guts. Both species did consume a wide variety of food types. Particles from fungal origin were classified roughly. They consisted mainly of dark coloured hyphal fragments from dematiaceous Hyphomycetes (Fungi imperfecti) which could not be identified exactly, and structures associated with fungal reproduction, like conidia of *Penicillium* and *Aspergillus* species. Also various amounts of green algae (*Pleurococcus* spec.) and pollen (*Pinus*, *Betula*) were found. Other materials from higher plants, detritus and mineral particles were very scarce. Apart from the remnants of exuviae of *T. minor* occasionally present in the guts of this species, none of the food items were found exclusively in one species. Food composition varied in space and time, and between individuals but, on the average, the guts of *O. cincta* always contained a larger proportion of green algae. This can be seen in Fig. 2 where the mean composition of the gut contents of both species from each sample is presented in a triangular diagram.

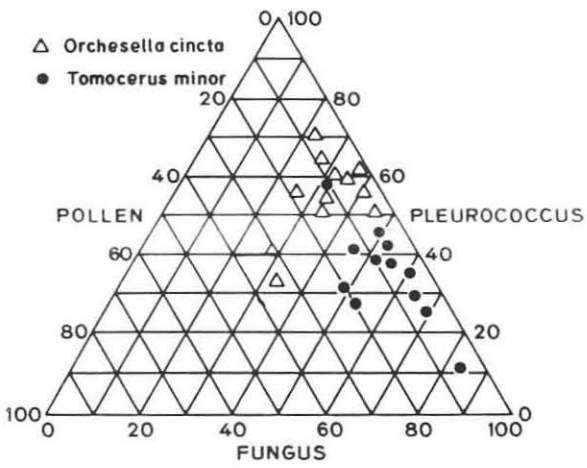

Fig. 2. Mean composition of the gut contents of *O. cincta* and *T. minor*. Each entry is a mean of 10 animals. The axes of the diagram denote the percentage of the three main categories of food observed in the gut contents.

The gut contents of *T. minor* and *O. cincta* from laboratory cultures were almost identical. Since both species were fed with the same mixture of fungi and green algae, any preference should result in a different percentage of green algae in their guts. The mean percentage green algae was 65% (S.D. = 4%) for *O. cincta* and 62% (S.D. = 5%) for *T. minor*. This result, and the fact that none of the food items observed in field animals are found exclusively in one species indicates that differences in the diets of these species in the field might reflect differences in microhabitat selection.

3.2. Spatial distribution

According to the analysis displayed in Table 1, trees have a significant effect on the total density of *O. cincta* and *T. minor*. The effect appears to be the same on both species, since the species × tree interaction was not significant. The effect of location is not significant either, indicating that total springtail density in the edge area is as high as in the central part. Species composition is different, however, as demonstrated by the significant species × location interaction. The overall pattern of effects and interactions is visualized in Fig. 3: *O. cincta* is the dominant species at the edge, and *T. minor* in the central area.

No effects of trees nor location could be observed in springtail predators. Moreover population density of predators was only weakly correlated with springtail density ($r = +0.25$).

The results from the sampling of the transects (see Fig. 1) are shown in Fig. 4. The mean number of individuals of each species present in a 10 cm diameter soil corer is plotted against the distance from the edge, measured in tree distances. So "2" on the abcis refers to the base of the second tree in the transects. All species except *T. minor* tend to decrease in abundance towards the centre of the woodland, on both sampling occasions. Again, the springtail predators extracted from the samples did not show any pattern that could be related to differences in distribution of their prey.

The slopes of the regression lines (regression coefficients) shown in Fig. 4. appear to be species specific, and can be related to the drought resistance of the species, as measured by their transpiration rates (Table 2). When the regression coefficients are plotted against the reciprocal of the corresponding transpiration rates (tentatively labeled "cuticular resistance") two almost perfect linear relations appear (correlation coefficient < -0.99), displayed in Fig. 5. Unfortunately, due to the smaller samples used in summer, a regression coefficient for the sparsely occurring species *L. violaceus* could not be computed, since it should fall rather nicely between *O. villosa* and *O. cincta*.

Table 1. ANOVA table of springtail numbers per 10 cm ⌀ core sample

Source of variation	Sum of squares	d.f.	Mean square	F ratio
I. Between samples (total)	49.554,99	35		
Effect of location	2.429,78	1	2,429,78	2.49 n.s.
Effect of trees	14.047,52	1	14.047,52	14.40***
Trees × location interaction	1.862,90	1	1.862,90	1.91 n.s.
Between samples within groups	31.214,79	32	0.975,46	
II. Within samples	49.566,52	36		
Effect of species	1.046,61	1	1.046,61	1.21 n.s.
Species × location interaction	20.239,48	1	20.239,48	23.43***
Species × tree interaction	0.380,88	1	0.380,88	0.44 n.s.
Species × tree × location interaction	0.251,54	1	0.251,54	0.29 n.s.
Species × error within	27.648,01	32	0.863,7	

d.f.: degrees of freedom; n.s.: not significant; ***: significant at $\alpha = 0.001$.

Note: The analyses evaluates the effects of location (edge vs. centre), trees and the difference between *O. cincta* and *T. minor* (effect of species).

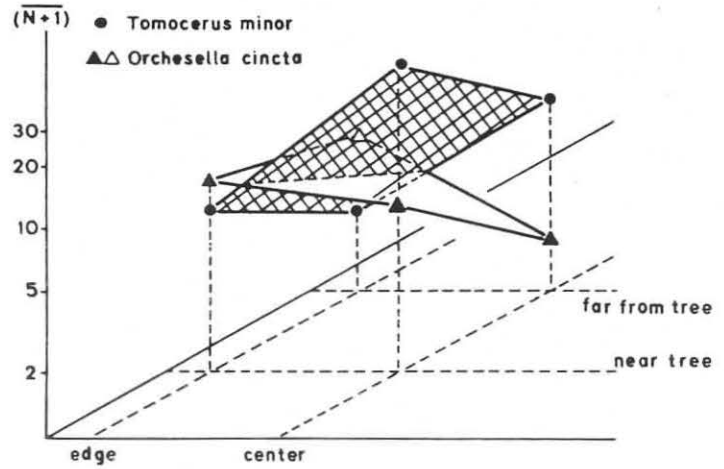

Fig. 3. Diagram illustrating the effect of trees and edge vs centre of the woodland on density of *O. cincta* and *T. minor*. Density is represented on a logarithmic scale, and is the backtransformed mean of ln (N + 1) transformed sample counts for each factor combination.

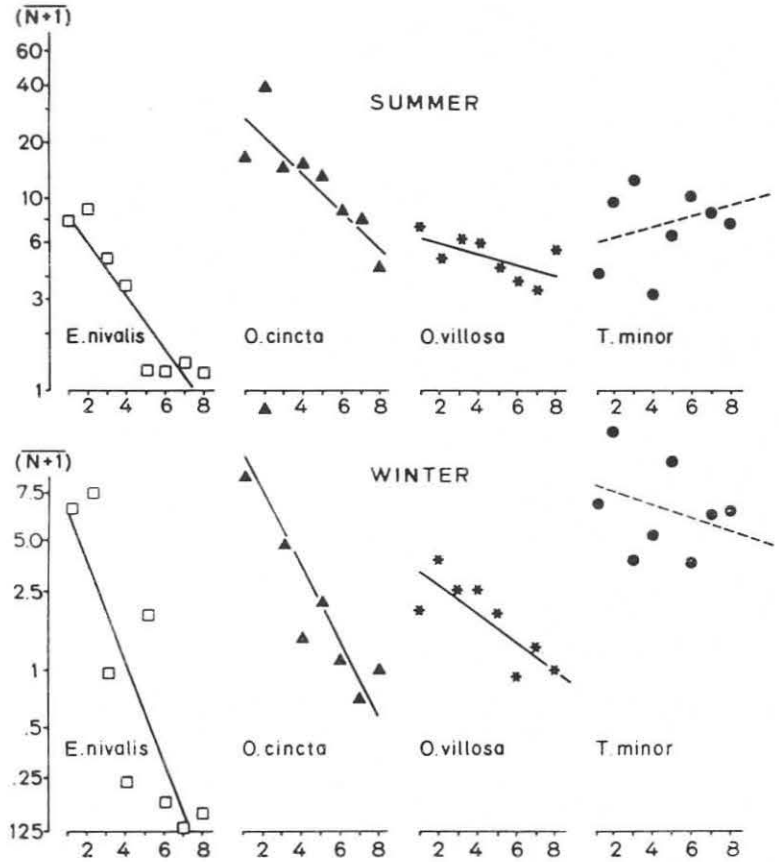

Fig. 4. Relation between distance from the edge of the woodland and population density of springtails per 10 cm ⌀ soil core, in summer and winter.

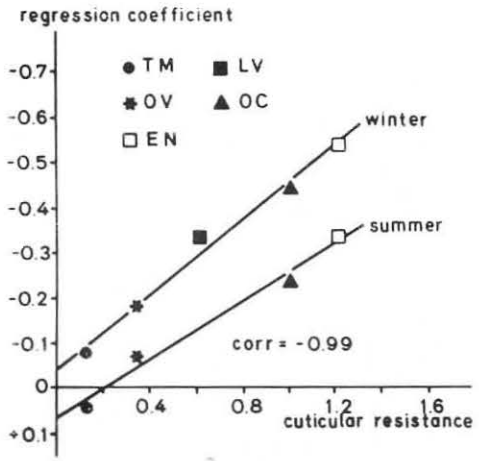

Fig. 5. Relation between the regression coefficients from Fig. 4 and the reciprocal or weight specific transpiration rate at 18 °C and 0% R.H. (cuticular resistance).

Table 2. Transpiration rate in μg/mg/min at 18 °C and 0% R.H.); regression coefficient and ratio of winter and summer population density

Species	Transpiration rate	Regression coefficients		winter density
		summer	winter	summer density
T. minor	8.48	+0.05	—0.08	97%
O. villosa	2.93	—0.07	—0.18	39%
L. violaceus	1.67	—	—0.33	—
O. cincta	1.00	—0.23	—0.43	20%
E. nivalis	0.83	—0.33	—0.54	28%

Another trend apparent from Fig. 4 is a difference in species composition between summer and winter. In summer *O. cincta* seems dominant, in winter *T. minor*. To examine this phenomenon in more detail the ratio of mean winter and mean summer population density was computed for each species. The results are shown in Table 2. The mean population density of *T. minor* is rather constant but the population densities of the other species decrease markedly. The decrease of population density of each species is again highly correlated ($r = 0.992$) with transpiration rate of its individuals, indicating that species with permeable integuments survive better or produce more offspring during autumn.

4. Discussion

Since differences in food selection between *O. cincta* and *T. minor* were not observed it was concluded that differences in gut content of field animals reflect differences in spatial distribution. The higher proportion of *Pleurococcus* spec. in the guts of *O. cincta* is in agreement with published data on other *Orchesella* or *Tomocerus* species (DE BERNARDI & PARISI 1968, ANDERSON & HEALEY 1972) and might indicate a more surface dwelling way of life, a conclusion also drawn by ANDERSON & HEALEY (1972). Differences in vertical distribution of *O. cincta* and *T. minor* were observed by VERHOEF (unpublished) using seminatural litter layers in an experimental situation. *T. minor* was restricted to the moist deeper layers, whereas *O. cincta* was more or less uniformly distributed over the profile, as could be expected from its lower transpiration rate.

Bödvarsson (1970) and Petersen (1980) looked at the relation between diets and vertical distribution in a more general way, in Petersen's (1980) words: "The euedaphic species are obliged to feed more or less continuously on a poor food, whereas the epedaphic species as the other extreme must spend much time and energy in search for better quality foods."

This generalisation was based on the fact that in euedaphic species the proportion of animals with filled guts is on the average higher than in surface-dwelling species. Although a low proportion of filled guts can sometimes be related to a low availability of food during dry periods (Joosse & Testerink 1977), the average proportion of filled guts in a population reflects the proportion of moulting individuals, which depends on the moulting rate of the species considered (de With & Joosse 1971). Thibaud (1977) accumulated a massive amount of data on the moulting rate of Collembola, permitting the conclusion that euedaphic species have on the average a much lower moulting rate than surface-dwelling life forms. The proportions of filled guts in *O. cincta* and *T. minor* in this study are in agreement with this pattern: Compared to *O. cincta*, *T. minor* has a lower moulting rate (Joosse & Veltkamp 1970), a higher proportion of filled guts and seems to prefer deeper litter layers.

The marked differences in horizontal spatial distribution of individuals of all springtail species in this study were strongly related to their transpiration rate. Relations between transpiration and habitat moisture are not unusual and can be found in any arthropod class (Edney 1977), but the patterns observed here cannot be explained by drought tolerance alone. Clearly, the most drought sensitive species, *T. minor*, appears to be less exacting in the choice of its habitat than the drought tolerant *O. cincta* and *E. nivalis*. Since this distribution pattern is more pronounced in winter (lower regression coefficients, see Table 2 and Fig. 5), an explanation based on interspecific competition is not very reasonable. At lower temperatures, interactions between poikilothermic animals will not be very important. It seems therefore tempting to conclude that these distribution patterns are created by important abiotic factors in the environment and physiological limitations of a species.

The strong decrease in abundance of drought tolerant species in autumn suggests that low temperatures are less favourable for these animals. *O. cincta* is less able to sustain growth and reproduction at lower temperatures than *T. minor* (Vegter in prep.), but the effect of temperature on these processes is stronger in *O. cincta*. Similar effects were observed for the moulting rate of these species by Joosse & Veltkamp (1970). The analysis of seasonal dynamics of *O. cincta* and *T. minor* in the field by van Straalen (1983) revealed that fertility of *O. cincta* was higher compared to *T. minor*. *O. cincta* might achieve this by exposing itself to higher temperatures. On the other hand, mortality was also higher in *O. cincta*. The higher activity of individuals of this species makes them more vulnerable to predation (Ernsting & Jansen 1978), a very important mortality factor in springtails (Ernsting & Joosse 1974). When mortality is as high at the edge as in the central area of the woodland, *O.* cincta might be able to attain higher population levels at the edge, where the temperature in the top layer of the litter is higher due to indirect insolation. Although this hypothesis is in agreement with all observations, the assumption that mortality of *O. cincta* is only weakly influenced by temperature must hold. Moreover, to explain the distribution of other species in the same way would require a delicate balancing of transpiration rate and temperature dependence of fertility and mortality.

A possible harmful effect of high moisture on drought tolerant species might provide an alternative, and perhaps additional explanation. When, during rainy periods, moisture in the litter layer is high, many springtails can take refuge on tree trunks (Bowden *et al.* 1976, Bauer 1979 and Vegter unpublished). This phenomenon makes the concentration of springtails around trees, as observed in this study and by Stebayeva (1975), more understandable. Bauer (1979) showed that the propensity of a springtail species to climb trees depends on its drought tolerance, and stated that the prime function of tree climbing was to graze on epiphytic green algae. Although Bauer's hypothesis is in accordance with

the observations on gut contents presented in this paper, it depends critically on the assumption that springtails feed preferentially on epiphytic fungi and green algae, or that food in the litter layer is always limiting. Avoidance of excessive moisture is more likely, and the opportunity to feed on easily accessible food on the tree trunk might just be a lucky coincidence.

Apart from the gradual change in abiotic regime from the edge to the centre of the woodland, a similar variation in abiotic factors is present from the top layer of the litter to the soil. This trend in the abiotic environment is parallelled by a trend in a large number of morphological and physiological characters when surface dwelling springtails are compared with their deeper living relatives (see PETERSEN 1980). This suggests that different selective pressures operate at different levels in the soil profile, leading to segregation of niches of major groups of springtail species, mainly along a vertical habitat gradient. Within groups of species sharing the same depth in the profile, resource partitioning might occur along other dimensions.

Clear differences in food selection between species are at present only known for hemiedaphic fungivore species (see references in USHER *et al.* 1982), which are uniformly distributed in space, because variation in abiotic factors deeper in the soil is lower. On the other hand surface dwelling species are confronted with higher spatial variation in abiotic factors, giving rise to differences in spatial pattern. Moreover, the effects of seasonal variation are more pronounced in the top layer of the litter.

The seasonal temperature regime can give rise to considerable seasonal variation in population numbers, which in the extreme can lead to an almost complete segregation of species in time, as shown by the different phenology of the closely related species *Tomocerus flavescens* (TULLBERG) and *Tomocerus longicornis* (MUELLER). *T. flavescens* reproduces in summer, whereas *T. longicornis* produces overwintering eggs that hatch the next spring. These patterns are very different from the high seasonal synchrony of deeper living springtails observed by USHER *et al.* (1979).

In the species studied in this paper, habitat differences seem to prevail. The relation between transpiration rate and spatial pattern of individuals of a species suggests that water relations are of overwhelming importance in the delimitation of fundamental niches between species. The rather even spacing of "cuticular resistance" (see Fig. 5) is even reminiscent of the idea of "overdispersion of niches" (SCHOENER 1974).

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VEGTER, J. J., 1982. Food and habitat specialisation in coexisting springtails (Collembola, Entomobryidae). Pedobiologia **25**, 253—262.

Spatial distribution of surface-dwelling springtail species was studied in a pine plantation. Whereas *Orchesella cincta* was more abundant near the edge of the plantation, *Tomocerus minor* was more abundant in the central area. A closer examination revealed a zoned distribution.

Abundance of *Entomobrya nivalis*, *Orchesella cincta* and *Orchesella villosa* decreased from the edge to the centre. The decrease was highest for *E. nivalis* and lowest for *O. villosa*. No zonation pattern was found for *T. minor* and for predators on springtails. Gut contents of the two dominant species, *O. cincta* and *T. minor*, were different in the field, but not in laboratory experiments, indicating a difference in microdistribution for individuals of these species. The role of abiotic factors and interspecific interactions in the formation of these patterns will be discussed.

Key words: Collembola, Entomobryidae, food, habitat, specialisation, spatial distribution, gut content, microdistribution.